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Year: 2015

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## **Hot spots of mutualistic networks**

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DOI: <https://doi.org/10.1111/1365-2656.12304>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-120825>

Journal Article

Accepted Version

Originally published at:

Gilarranz, Luis J; Sabatino, Malena; Aizen, Marcelo A; Bascompte, Jordi (2015). Hot spots of mutualistic networks. *Journal of Animal Ecology*, 84(2):407-413.

DOI: <https://doi.org/10.1111/1365-2656.12304>

# Hotspots of Mutualistic Networks

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RUNNING HEADLINE: Hotspots of Mutualistic Networks.

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# Abstract

Incorporating interactions into a biogeographical framework may serve to understand how interactions and the services they provide are distributed in space. We begin by simulating the spatiotemporal dynamics of realistic mutualistic networks inhabiting spatial networks of habitat patches. We proceed by comparing these predictions with the empirical results of a set of pollination networks in isolated hills of the Argentinian Pampas. We first find that one needs to sample up to five times as much area to record interactions as would be needed to sample the same proportion of species. Second, we find that peripheral patches have fewer interactions and harbor less nested networks —therefore potentially less resilient communities— compared to central patches. Our results highlight the important role played by the structure of dispersal routes on the spatial distribution of community patterns. This may help to understand the formation of biodiversity hotspots.

## KEYWORDS:

Island biogeography, Metacommunities, Nestedness, Spatial networks, Species-area relationship, Pollination, Seed-dispersal

# 1 Introduction

2 Biogeography attempts to describe the patterns of species distribution across  
3 geographical areas and has a long tradition in ecology and evolutionary biology, with  
4 early predecessors as influential as Alfred Russell Wallace. The publication of MacArthur  
5 and Wilson's book on island biogeography (MacArthur & Wilson, 1967) constituted a  
6 formidable theoretical framework that brought a predictive ability to determine the  
7 number of species on an island given its area and isolation. This, in turn, became a useful  
8 tool in conservation biology, as for example in the problem of choosing between a single  
9 large or several small (SLOSS) reserves (Higgs & Usher, 1980; Simberloff & Abele, 1976;  
10 Diamond, 1975; Bascompte *et al.*, 2007). The bridge to real-world conservation  
11 applications has even become stronger around the concepts of metapopulations (Hanski,  
12 1998) and metacommunities (Leibold *et al.*, 2004). Despite this success, traditional island  
13 biogeography dealt exclusively with species, ignoring their mutual dependencies. This  
14 approach resembles the development of the kinetic theory for ideal gases in physics, which  
15 initially also neglected interactions (Alonso, Etienne & McKane, 2006; Volkov *et al.*,  
16 2007).

17 Almost independently of the above efforts in describing how species are distributed in  
18 space, recent progress has made explicit that species interactions are an equally  
19 important component of biodiversity. Interactions are at the core of significant ecosystem  
20 services such as pollination or biological control. The way these interactions are arranged  
21 to create networks of interacting species largely affects the persistence of these networks  
22 and the number of species they can support (Memmott, Waser & Price, 2004; Burgos  
23 *et al.*, 2007; Okuyama & Holland, 2008; Bastolla *et al.*, 2009; Thébault & Fontaine,  
24 2010). In the context of global change, species interactions have also been found to be  
25 even more susceptible than species themselves (Janzen, 1980; Tylianakis *et al.*, 2008;

1 Sabatino, Maceira & Aizen, 2010). The disruption of interactions may in turn foresee  
2 future species losses (Aizen, Sabatino & Tylianakis, 2012).  
3 A subsequent step, therefore, seems to be the inclusion of species interaction networks  
4 into a biogeographical framework. An early contribution in this direction has been John  
5 N. Thompson's geographic mosaic theory of coevolution (Thompson, 2005). This theory  
6 has brought a geographic dimension to studies on the coevolution among free-living  
7 species. For example, it has described how the sign and strength of interactions between  
8 small groups of species depend on the local presence of other species. The influence of  
9 both the geographic mosaic and early metapopulation theory lead to the development of  
10 metacommunity theory, which addresses the spatial distribution of small sets of  
11 ecologically interacting species (Leibold et al., 2004). The first studies on  
12 metacommunities were mainly theoretical descriptions of trophic modules, with very few  
13 studies describing an entire, realistic ecological network. Only recently, there have been  
14 significant steps in this direction (Olesen & Jordano, 2002; Brose *et al.*, 2004; Fortuna &  
15 Bascompte, 2006; Sabatino, Maceira & Aizen, 2010; Sugiura, 2010; Gravel *et al.*, 2011;  
16 Pillai, Gonzalez & Loreau, 2011; González-Castro, Traveset & Nogales, 2012;  
17 Trøjelsgaard *et al.*, 2013). As deviations from the behavior of ideal gases improved the  
18 kinetic theory (Alonso, Etienne & McKane, 2006; Volkov *et al.*, 2007), consideration of  
19 interactions has been shown to improve the accuracy of the predictions of the species-area  
20 relationship (Brose *et al.*, 2004; Gravel *et al.*, 2011). So far, however, the focus has been  
21 in correcting estimates of number of species (Brose *et al.*, 2004; Gravel *et al.*, 2011; Jabot  
22 & Bascompte, 2012), and unifying two previously unrelated scaling laws, i.e., the  
23 species-area and the interaction-species relationships (Brose *et al.*, 2004; Aizen, Sabatino  
24 & Tylianakis, 2012). The few studies explicitly addressing mutualistic interactions among  
25 species on a biogeographical scale have explored their dependence on island area  
26 (Sugiura, 2010) or age (Trøjelsgaard *et al.*, 2013).

1 This exciting progress, therefore, still leaves unanswered the question of how interactions  
2 and the networks they form are distributed across heterogeneous landscapes. A question  
3 that, if answered, will provide insight on the relative role of regional and local processes in  
4 shaping biodiversity. This would allow us, for instance, to achieve a better understanding  
5 of where and how regional biodiversity hotspots are formed and maintained.

6 Here we tackle this problem by using a metanetwork approach where species interaction  
7 networks inhabit a spatial network of habitat patches (Fig. 1). We first present a general  
8 framework based on extensive simulations. This allows controlling both the structure of  
9 local interactions and that of spatial sites. We then compare these broad predictions with  
10 the results for a particular case study formed by 12 pollination networks from untiled  
11 hills or “sierras” raising in the Pampa region in Argentina (Sabatino, Maceira & Aizen,  
12 2010). This will show to what extent patterns predicted by our theoretical framework are  
13 found in nature. In this context, we change the emphasis of biogeography from species to  
14 their interactions, and look into the biogeographical patterns of such interactions.

15 We ask whether interactions are relevant enough to modify conservation policies. For  
16 that, we begin by answering the question of how many patches need to be conserved to  
17 register a given fraction of species or interactions. Next, we explore how these  
18 interactions are distributed across the different habitat patches. This has the potential to  
19 be used as a prioritization tool. Finally, we scale all the way up to interaction networks  
20 to describe how network structure changes across the landscape. This later scale of  
21 resolution will allow us to assess the interplay between spatial and local dynamics in  
22 shaping regional patterns of biodiversity.

## Materials and methods

### Dispersal, colonization, and survival

Metacomunity dynamics are simulated by a random process where species can colonize empty patches and be driven locally extinct. Every time step is divided into a colonization and an extinction phase. Roughly speaking, we use a spatially explicit version of the model described in Fortuna & Bascompte (2006). A patch is either empty or occupied. The model has two parameters, a colonization and an extinction probability. Patches where a certain species is absent can be colonized by that species with a probability  $c$ . Similarly, a species present in a certain patch can go extinct with a probability  $e$ . The probability of a patch  $p$  being colonized by species  $s$  is given by the following equation:

$$C(p, s) = 1 - (1 - c)^a, \quad (1)$$

where the exponent  $a$  depends on whether species  $s$  is an animal or a plant. If the former,  $a$  is equal to the number of adjacent patches where that animal is present. Adjacent patches are those with a direct dispersal route to the focal patch  $p$ . Nevertheless, animals only live where they can find food. Therefore, if in patch  $p$  there were none of the plant species on which animal  $s$  feeds, the probability of animal  $s$  to colonize patch  $p$  would be zero. If species  $s$  is a plant in a plant-pollinator network, the exponent  $a$  is equal to the number of adjacent patches where that plant is present.

Besides each animal species having a certain probability of becoming locally extinct, they go deterministically coextinct if every plant species they feed on has become extinct in that habitat patch.

The extinction probability for animals is the same for all species and all patches

1  $E(p, s) = e$ . Regarding plants in plant-pollinator metacomunities, their extinction  
2 probability depends on their number of pollinators present in that given patch  $b$ . This is  
3 encapsulated in the following equation for a plant's extinction probability:

$$E(p, s) = e/b. \quad (2)$$

4 Note that all probabilities are taken from a uniform distribution.  
5 Despite the extreme simplicity behind these simulations, the model reproduces  
6 qualitatively the patterns observed in nature. Thus, we can argue that these simple rules  
7 are just enough to encapsulate the essence of the metacommunity dynamics.

## 8 **Spatial Networks**

9 We compare four different spatial structures of increasing heterogeneity in the number of  
10 links per habitat patch: a regular lattice, a random network (Erdős & Rényi, 1959), an  
11 exponential network (following Barabasi & Albert (1999) with uniformly random  
12 attachment), and a scale-free network (following Barabasi & Albert (1999) with  
13 preferential attachment). All theoretical results presented in main text correspond to the  
14 random network, while we reproduce the equivalent results for the other spatial  
15 topologies in the Appendix S1. This comparison serves to test to what degree spatial  
16 structure affects the patterns here described. The advantage of using large theoretical  
17 networks relies in the statistical power they provide and in our ability to control for  
18 spatial heterogeneity.

19 The empirical dataset consists of 12 patches out of 18 from which we know the local  
20 plant-pollinator networks. The spatial network in this case is constructed by using a  
21 threshold distance under which two patches are considered to be linked through dispersal  
22 (Urban & Keitt, 2001). Here we use the thresholds that maximize the signal between the



measured property and patch centrality (see Appendix S4 for details and an assessment of the robustness of our analysis to this particular choice). In the construction of the empirical spatial network we include all the 18 fragments. Although we do not sample the other 6, they can be part of one or many dispersal routes.

As a measure of the importance of a habitat patch within the spatial network, we focus on its betweenness centrality. A patch's betweenness centrality measures the number of times such a patch acts as a bridge along the shortest path between two other patches (Freeman, 1977). This measure is intimately linked to dispersal within the network. Note that this encapsulates the concept of isolation in MacArthur and Wilson's theory of island biogeography. Thus, our work expands the few recent papers addressing networks in a biogeographical dimension by adding a patch's isolation and spatial dynamics to the previous focus on island area (Sugiura, 2010) and age (Trøjelsgaard *et al.*, 2013).

## Ecological Networks

The Pampean plant-pollinator networks were surveyed from 12 isolated "sierras," ranging between 12 and 2147 ha and immersed in an intensively-used agricultural matrix. The number of plant species, animal species, and interactions ranged between 17 and 39, 48 and 79, and 132 and 243, respectively. Further details can be found in Sabatino, Maceira & Aizen (2010) and Aizen, Sabatino & Tylianakis (2012). For the simulations, we use the meta-web of these local networks, composed by 172 pollinators and 96 plants.

In our simulations, each patch of the spatial network harbors an empirical plant-pollinator network. It depicts the mutualistic interactions between plants and the animals that pollinate their flowers. The characteristics of those networks are described in Bascompte & Jordano (2007). In particular, at the beginning of the simulation we populate each habitat fragment with the metaweb from Sabatino, Maceira & Aizen (2010).

To see whether our results affect only plant-pollinator networks, or they are general to

1 mutualistic interactions, we have also simulated the dynamics of plant-seed dispersers.  
2 Both the details of the simulations and the results can be found in the Appendix S2. All  
3 qualitative results shown here hold for this other set of simulations.  
4 As a measure of overall network structure, here we focus on nestedness. In a nested  
5 network, specialists interact with species that form well-defined subsets of the species  
6 interacting with the most generalists (Bascompte *et al.*, 2003). This is a pervasive  
7 property of the architecture of mutualistic networks, with potential implications for their  
8 persistence (Memmott, Waser & Price, 2004; Burgos *et al.*, 2007; Bastolla *et al.*, 2009).

## 9 Measure of Nestedness

10 Nestedness is measured as in Bastolla *et al.* (2009), which has the advantage of being  
11 related to network dynamics. Although there are other nestedness measures such as  
12 NODF (Almeida-Neto *et al.*, 2008), they are all highly correlated and do not qualitatively  
13 change our results (Bascompte & Jordano, 2014). To measure relative nestedness, we  
14 randomized the network a thousand times using the probabilistic model described in  
15 Bascompte *et al.* (2003). Relative nestedness was then calculated as a  $z$ -score between  
16 the observed value and the randomizations (Eq. 3).

$$z = \frac{N - \overline{N}_r}{\sigma_{N_r}}, \quad (3)$$

17 where  $N$  is the nestedness value of the observed network, and  $\overline{N}_r$  and  $\sigma_{N_r}$  are the average  
18 and standard deviation of nestedness values across randomized network replicates.

## 19 Results

20 Our results show that one needs to sample a larger number of patches to record  
21 interactions than would be necessary to record an equal proportion of species (Fig. 2).

1 This difference is largely modulated by both environmental stochasticity—here  
 2 represented by the extinction-to-colonization ratio—and spatial heterogeneity—here  
 3 represented by the degree distribution of the spatial network (Appendix Fig. S1).  
 4 Specifically, the larger the environmental stochasticity, the larger the number of habitat  
 5 fragments that have to be sampled to achieve an equivalent proportion of interactions  
 6 (Appendix Fig. S2). This difference also grows with the heterogeneity of the spatial  
 7 network. Thus, for the random spatial network (Appendix Fig. S1) one would need to  
 8 sample 1.7 times more patches at the highest value of environmental stochasticity. This  
 9 difference grows up to 2.5 times more patches for the scale-free network (Appendix Figs.  
 10 S2). In agreement with these theoretical results, the study of the empirical dataset shows  
 11 that—for this particular setting—one would need to sample twice the number of patches  
 12 to record 60% of the interactions than to record 60% of the species (Fig. 2).  
 13 Once we have shown how the total number of interactions scales up with number of  
 14 patches—that can be taken as surrogate of area in our model, we next move to mapping  
 15 how the number of interactions is distributed across the spatial network. This will inform  
 16 us on how the number of interactions depends on patch isolation. Our results show first  
 17 that more central patches—i.e., the more important ones in terms of dispersal across the  
 18 network (see Materials and Methods for a proper definition)—have more interactions and  
 19 more species than more isolated patches (as noted by the positive slopes in Fig. 3).  
 20 Second, the proportion of interactions in a patch—compared with the total number of  
 21 interactions in the metaweb—is always lower than the equivalent proportion of species  
 22 (as noted by the relative position of the two fitted lines in Fig. 3). This consistent  
 23 pattern explains the previous result, i.e., the fact that the rarefaction curve of species lies  
 24 above the rarefaction curve of interactions. This pattern is observed both in the  
 25 simulations and the analysis of the empirical dataset.  
 26 The above two results were based on counting the number of interactions and presenting

1 this result either as an aggregated, or a patch-by-patch amount. We next consider the  
2 patterning of these interactions in the context of how the nested structure of the local  
3 mutualistic networks changes across space (Fig. 4). As shown by our results, central  
4 patches sustain communities whose interactions are significantly nested, while peripheral  
5 patches harbor less nested communities with interactions organized in a way that does  
6 not differ significantly from a random assembly. Indeed, the more central the habitat  
7 patch is, the more significantly nested is its mutualistic community (Fig. 4). The same  
8 pattern is found in the empirical metacommunity. In the Appendix S3 we show that the  
9 relationship between nestedness and patch centrality is not mediated by the relationship  
10 between network size and patch centrality. As also shown in the Appendix S5, patch  
11 centrality is a better predictor of the number of interactions and of network structure  
12 than patch area. However, the number of species in a patch is more correlated with patch  
13 area than with patch centrality.

## 14 Discussion

15 A predictive theory of how interactions are distributed in space may be relevant in the  
16 context of understanding how habitat fragmentation will erode the architecture of  
17 biodiversity and the services it provides. Specifically, knowing how this network structure  
18 changes across the landscape can provide insight on how resilient these networks will be.  
19 Similarly, it can guide efforts aimed at reversing this destructive trend, such as in reserve  
20 design.

21 The species-area relationship has been a cornerstone of a predictive conservation biology  
22 in the sense of exploring how different re-arrangements of the habitat would translate into  
23 different numbers of coexisting species. This can provide a rule of thumb in terms of how  
24 much area should be protected if we were interested in conserving a minimum number of

1 species. In line with this, here we show that we may need as much as five times more  
2 habitat patches in order to preserve a given proportion of total interactions, specially in  
3 most fluctuating environments. This means that a reserve arrangement designed on the  
4 basis of species presences and absences may not be enough to protect interactions, and  
5 therefore will fail in protecting ecosystem functioning (Tylianakis *et al.*, 2009).  
6 In spatial networks of habitat patches, however, not all patches are equally relevant in  
7 order to preserve interactions. We have shown that there is considerable variability in the  
8 importance of a given patch in terms of harboring interactions and species. That  
9 importance depends on the patch location in relation to the rest of the patches.  
10 Therefore, this result should be interpreted in the light of the differential rescue effect  
11 across the landscape, which is linked to patch position. Even when the extinction rate of  
12 a species was the same, the rescue effect by which a local patch can be recolonized from a  
13 nearby patch is much lower in peripheral patches (Gilaranz & Bascompte, 2012).  
14 However, not only is the distribution of species heterogeneous across the landscape. As  
15 recently pointed out, in real landscapes there is not a random loss of interactions; while  
16 interactions between generalist species are ubiquitous, interactions involving specialist  
17 species are much more vulnerable (Aizen, Sabatino & Tylianakis, 2012). Interestingly  
18 enough, this type of result can only be understood when integrating information on local  
19 network structure and landscape dynamics. This relates to two major theories bringing  
20 analytical tractability to multispecific coevolutionary studies: network theory (Bascompte  
21 & Jordano, 2007) and the geographic mosaic theory of coevolution (Thompson, 2005).  
22 Beyond differences in the number of interactions across the landscape, different patches  
23 are also playing different roles in terms of how their interactions are assembled. Thus, the  
24 nested structure of the local network varies across the landscape. Given the importance  
25 of nestedness for maintaining network size (Bastolla *et al.*, 2009) and robustness  
26 (Memmott, Waser & Price, 2004; Burgos *et al.*, 2007; Thébault & Fontaine, 2010), local

1 differences in nestedness are likely to translate into differences in the persistence of these  
2 local networks. The higher stability of communities in central patches is twofold. First,  
3 we have shown that central patches tend to harbor more nested communities. Other  
4 things being equal, nested communities tend to be more persistent (Bastolla *et al.*, 2009).  
5 Second, this goes along the tendency for such central patches to be involved in a large  
6 number of dispersal routes and therefore to have a higher incidence of rare species due to  
7 a higher recolonization rate.

8 Network persistence, therefore, is a combination of local and regional processes that  
9 cannot be understood independently from each other. The positive or negative feedbacks  
10 between patch isolation and network structure may help to explain the spatial  
11 distribution of biodiversity hotspots. These results pave the road for a deeper  
12 understanding of how spatial structure and dispersal simultaneously affect local  
13 community structure, the geographic distribution of ecosystem services, and  
14 coevolutionary processes.

## Acknowledgements

We would like to thank M.A. Fortuna, D.B. Stouffer, R.P. Rohr, S. Saavedra, and V. Dakos for fruitful discussions. J. Tylianakis and L. Harder made useful suggestions to previous versions of this draft. Research was funded by the European Research Council through an Advanced Grant (to JB), the Spanish Ministry of Education through a FPU PhD Fellowship (to LJG), and the National Institute of Agricultural Technology (INTA-PNECO1302), the Argentina National Research Council (CONICET-PIP 01623), the National Fund for Research (FONCyT-PICT 01300), and the National University of Comahue (UNC-B152/04) (to MS and MA).

## Data Accessibility

Data will be made available in a public repository such as Dryad Digital Repository once the paper is accepted. However, it is accessible to reviewers upon request.

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## **The following Supporting Information is available for this article online**

Appendix S1: Plant-pollinator interactions.

Appendix S2: Seed-disperser interactions.

Appendix S3: Nestedness increases with patch centrality independently of network size and connectance.

Appendix S4: Criteria to create the empirical spatial network.

Appendix S5: Influence of patch centrality and area.

## Figure captions

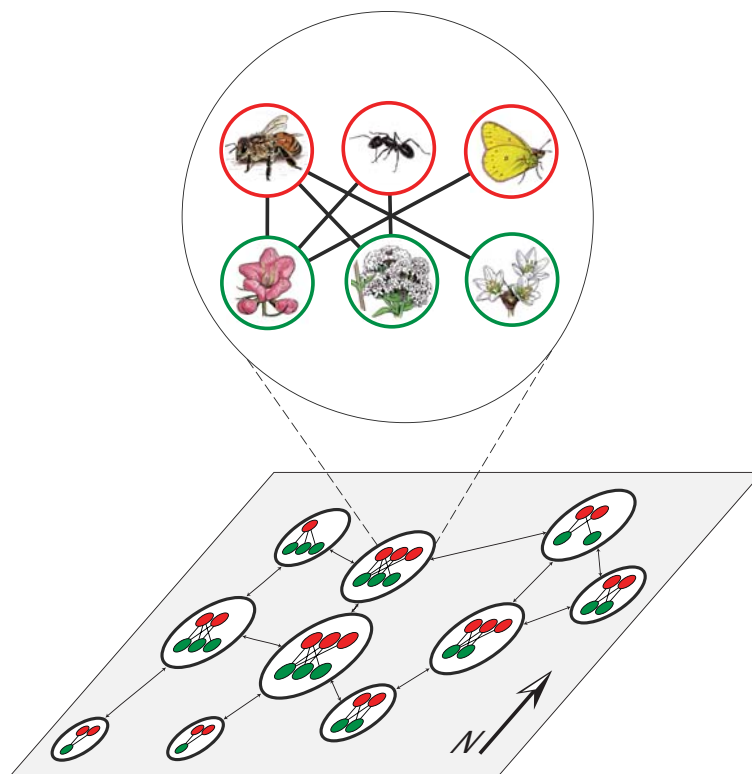


Figure 1: **Schematic representation of the theoretical framework developed in this manuscript.** Each patch of the spatial network (bottom) harbors a local mutualistic network (top). The figure depicts a subset of the metaweb described in Sabatino, Maceira & Aizen (2010). Pollinator species are, from left to right, *Apis mellifera*, *Camponotus sp.*, and *Colias lesbia*. Plant species are, from left to right, *Gerardia genistifolia*, *Stevia satureiifolia*, and *Nothoscordum bonariense*. Drawings by J. López Rojas.

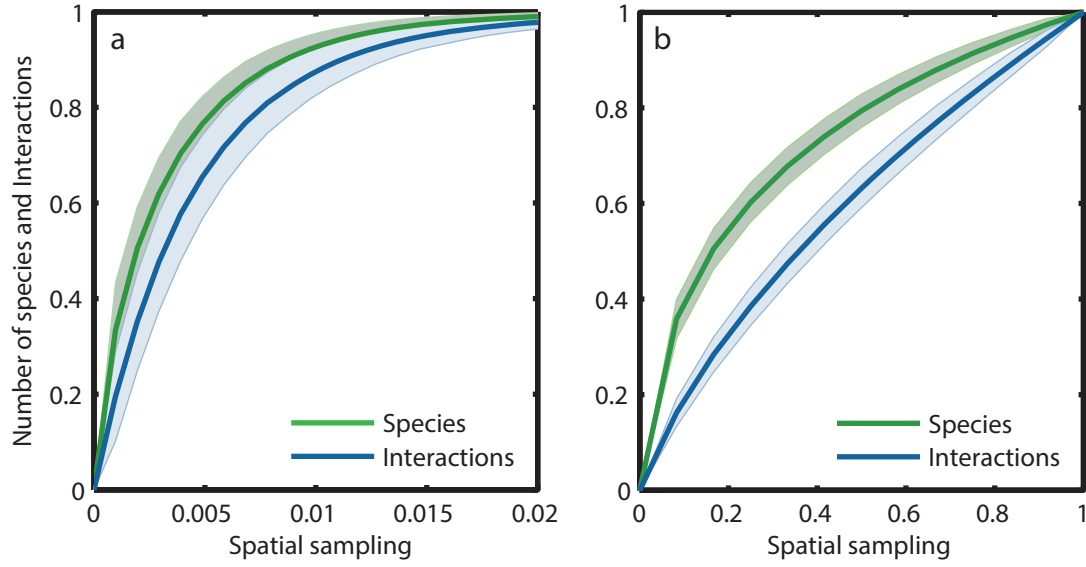


Figure 2: **Rarefaction curves of (a) species (green) and (b) interactions (blue) for the metacommunity simulations, and for the empirical case study.** Spatial sampling is measured as the proportion of sampled patches. Here we use the proportion of sampled species and interactions, respectively, in order to obtain comparable magnitudes. To obtain panel (a) the model runs in a spatial network with a random degree distribution, 1,024 nodes, and an extinction-to-colonization ratio of 2.2. After 10,000 time steps, we randomly sample the patches and count the new species and interactions found. Panel (b) corresponds to the empirical case study. The empirical network has 18 nodes. The habitat patches are also selected randomly. Shaded areas represent the 95% confidence interval.

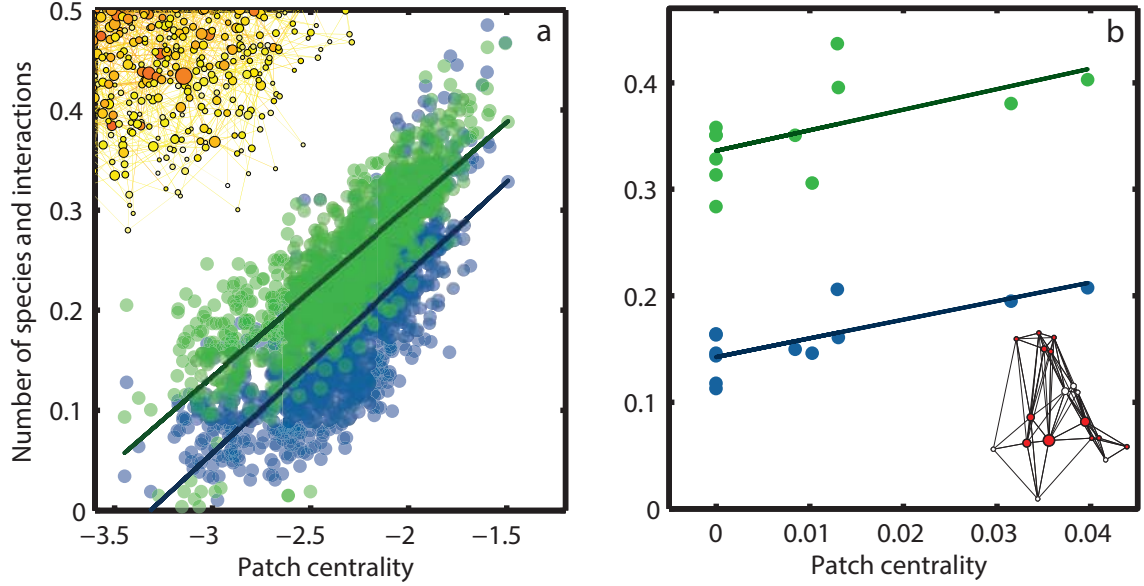


Figure 3: **Spatial distribution of species and interactions for the simulated (a) and empirical (b) metacommunities.** (a) The normalized number of species (green) and interactions (blue) is significantly correlated with the log betweenness centrality of the patch where the community is harbored (Spearman correlation,  $p < 0.001$ ,  $r = 0.80$  for interactions; and  $p < 0.001$ ,  $r = 0.85$  for species). In the top-left corner is shown a fragment of the theoretical network of 1,024 patches with a random degree distribution, and an extinction-to-colonization ratio of 2.2. The size of the nodes is proportional to their betweenness centrality, and the color is redder the larger is the number of interactions found in that patch. (b) The same result for the empirical case study ( $p = 0.016$ ,  $r = 0.67$  for interactions; and  $p = 0.019$ ,  $r = 0.66$  for species). The spatial network of the 18 patches with a threshold distance of 17 Km is represented in the bottom-right corner. Patches that were actually sampled are represented in red. The normalized number of species and interactions is calculated comparing the number found in the focal patch with the number of species or interactions found in the metaweb (Sabatino, Maceira & Aizen, 2010). Fitted lines are only meant to guide the eye.

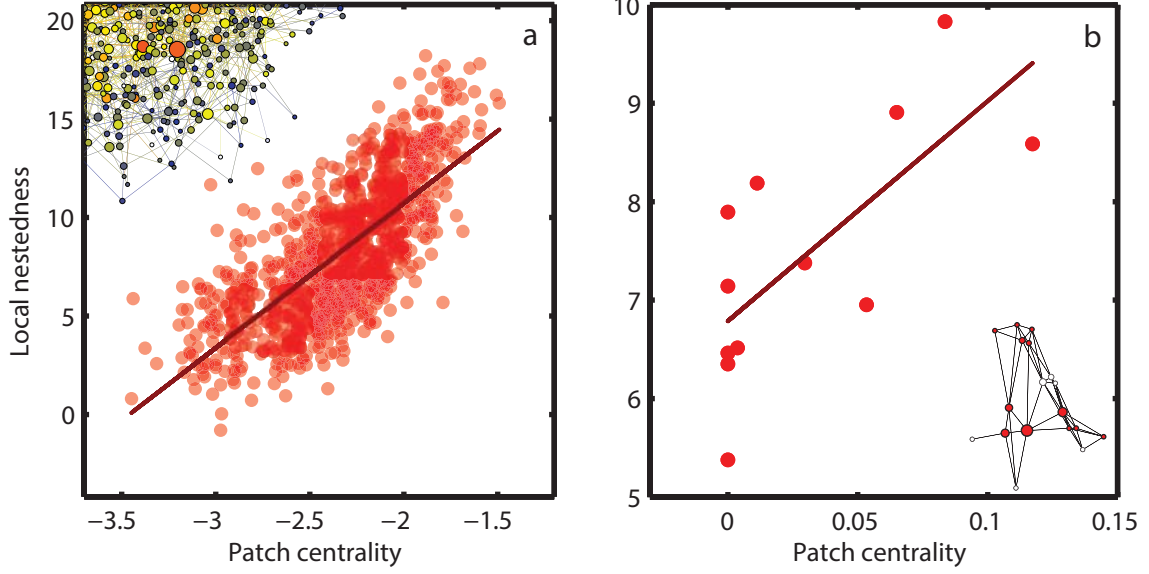


Figure 4: **Spatial distribution of network structure for the simulated (a) and empirical (b) metacommunities.** The average relative nestedness of a local community is significantly correlated with the log betweenness centrality of the patch where the community is harbored **(a)** (Spearman correlation,  $p < 0.001$ ,  $r = 0.74$ ). The results in here represent a random spatial network of 1,024 patches with an extinction-to-colonization ratio of 2.2. In the top-left corner we show a fragment of that spatial network. The size of the nodes is proportional to their betweenness centrality. White color indicates non-significantly nested networks ( $z\text{-score} \in [-1.96, \dots, 1.96]$ ). Blue/yellow/red scale represents significantly nested communities. The redder the node, the larger the nestedness of the community it harbors. **(b)** The same result for the empirical case study (Spearman correlation,  $p = 0.005$ ,  $r = 0.75$ ). The spatial network of the 18 patches with a threshold distance of 12 Km is represented in the bottom-right corner. Patches that were actually sampled are represented in red. Fitted lines are only meant to guide the eye.